TRACING THE ELUSIVE *HOLOPEDIUM GIBBERUM* IN THE PLANKTON OF LOCH NESS

JONATHAN GREY

Biological Sciences, IENS, Lancaster University, Lancaster, LA1 4YQ

INTRODUCTION

Loch Ness is the largest single volume of freshwater in the British Isles (~ 7.5 million m³) occupying a simple trench like basin 39 km long and 1.5 km wide. The steep shelving sides plunge to a maximum basin depth of 230 m and a mean depth of 132 m. The loch provides a useful reference as an undisturbed system because of its remote location and the relative lack of anthropogenic influence on the basin and its catchments. Considerable information has been compiled by the Loch Ness and Morar Project under the auspices of A. Shine and published in a volume of The Scottish Naturalist (1993). Freshwater ecologists from Lancaster University have been studying the loch for almost 10 years, initially characterising the microbial ecology of the loch and then focusing on the importance of allochthonous sources of carbon (derived from the catchment) as a subsidy to the production within the loch itself (Jones *et al.*, 1995, 1996, 1997, 1998; Laybourn-Parry *et al.*, 1994; Young *et al.*, 1995). Various aspects of the pelagic food web have now also been studied at the higher trophic levels including the fish species (Grey *et al.*, 2000a, b, Thackeray *et al.*, 2000).

Understanding the ecological role of crustacean zooplankton is fundamental to lake food web processes since the zooplankton links the microbial production to the fish. This article concerns the exclusively planktonic ctenopod ('comb-footed') *Holopedium gibberum* Zaddach. *Holopedium* is a relatively large species (mature specimens are 1.5 – 2.5 mm) which exhibits a strong preference for oligotrophic lakes with a low calcium content and drifts, or swims, supported by a gelatinous mantle (Scourfield & Harding, 1966). Gut content analysis of brown trout (*Salmo trutta*) provided by anglers from Loch Ness revealed little evidence of ingestion of Holopedium (Thackeray *et al.*, 2000). Thus, the apparent paradox of *Holopedium* occurring during the summer months with comparable abundance to other zooplankton species in the water column, yet rarely occurring in the diet of the planktivorous fish prompted a more detailed assessment of the ecology of this species in Loch Ness.

METHODS

Sampling was conducted monthly from a fixed station above a 200 m water column, from the northern end of Loch Ness. To investigate the water column structure, temperature readings at 5 m intervals from the surface to a depth of 50 m were recorded using a YellowStone Instruments probe, and the profiles plotted (Fig. 1). Plankton samples were also collected from the fixed station. Some horizontal variability in plankton distribution can develop in Loch Ness, mainly due to wind action (Jones *et al.*, 1995) but this does not seriously affect results from the fixed sampling station (Jones *et al.*, 1997). A 0.35 m diameter net of mesh size 110 (m was deployed taking three vertical hauls from 30 m to the surface and each sample was immediately preserved in 70 % industrial methylated spirit (IMS). Aliquots were examined in a Bogorov counting chamber using a Leica stereozoom microscope, the zooplankton identified to species level and mean abundance from the three replicate hauls calculated. Seasonal abundance patterns of individual zooplankton species were compared using regression analysis.

RESULTS

The water column temperature regime of Loch Ness was typical of a warm monomictic lake; a single period of free circulation per year, with consequent disruption of the thermocline. The water column was also relatively stable as one might expect from such a large volume of water ensuring only slow heat gain during spring (Fig. 1). Onset of stratification was delayed until June as a consequence of the colder waters and the prevailing south westerly winds blowing along the axis of the loch. The water column began to destabilise by late September.

The pelagic zooplankton from Loch Ness showed seasonal variation in both abundance and community composition, but was typically dominated by copepods (Fig. 2a). *Eudiaptomus gracilis* and *Cyclops abyssorum* and their associated naupliar juvenile stages were most abundant early in the year, peaking in May-June. Their combined abundance was >4 individuals per litre in early May. The cladocerans were generally less abundant (Fig. 2b), with *Bosmina coregoni* apparent in the water column throughout the year (0.05 – 0.1

individuals per litre), *Holopedium gibberum* appearing in May, peaking in July (<0.02 individuals per litre) and below detection from late September, and *Daphnia hyalina* dominating in late September and October. The large, predatory cladocerans, *Bythotrephes longimanus* and *Leptodora kindtii* both exhibited relatively short peaks of abundance around July, whilst *Polyphemus pediculus* attained highest numbers in September (Fig. 2c). The predators were comparatively rare, for the most part <0.01 per litre, but because of their larger size contributed substantially to zooplankton biomass during late summer (Grey *et al.*, 2000b). The abundance patterns of *Bythotrephes* and *Holopedium* were remarkably similar (r2 = 0.8; p = <0.01).

DISCUSSION

During the period of study, *Holopedium gibberum* was recorded in the water column of Loch Ness for approximately 4 – 5 months of the year at relatively low abundance (< 0.02 individuals per litre) compared to other grazing species comprising the pelagic zooplankton community. The patterns of abundance were consistent with those reported for Loch Ness by Maitland *et al.* (1981) from 1977-78. Zooplankton communities in oligotrophic lakes are usually dominated by the copepods, or by large cladocerans (Cyr, 1997). In Loch Ness, numerical dominance was associated with the copepods early in the season, but biomass dominance was attained by the cladocerans in late summer primarily due to the presence of the larger predatory species. The phytoplankton community of Loch Ness is typically dominated by large siliceous diatoms comprising *Asterionella* and *Aulacoseira* spp., whilst cryptomonad and rhodomonad flagellates become more abundant later in the summer when the water column is generally more structured (Jones *et al.* 1996; Jones unpublished data). Heterotrophic flagellates and bacterial production also tend to peak in late July – August (Laybourn-Parry & Walton, 1998). *Holopedium* are filter-feeders and most efficient at grazing on planktonic particles < 35 um in diameter (Cyr, 1997; Cyr & Curtis, 1999). Their appearance in the water column thus coincides with peaks in abundance of their putative prey, the smaller algae and bacterial flocs.

The mucopolysaccharide mantle of *Holopedium gibberum* may be well adapted to a life of drifting in the pelagic and indeed offer some defence against smaller predators (O'Brien *et al.*, 1979; Fryer, 1991; Lampert & Sommer, 1997) but must reduce survival against larger predators such as the planktivorous fish or indeed other predatory cladocerans. The mantle hinders escape mobility and the larger body size within increases the chance of visual detection due to the transparency of the mantle. The inherent contrast of a zooplankter is the key property determining how conspicuous the zooplankter is to a planktivore (Eggers, 1977). The

seasonal abundance of *Bythotrephes* was closely correlated with that of Holopedium in Loch Ness, suggestive of a strong predator : prey relationship. *Bythotrephes longimanus* is known to prey upon smaller individuals of *Holopedium* and can alter the size structure of the zooplankton community by increasing the relative abundance of larger bodied *Holopedium* in experimental mesocosms (Wahlström & Westman, 1999).

However, if predation pressure from cladocerans results in an increase in *Holopedium* body size, the converse is true of fish planktivores. In a study of Laurentian Shield lakes, Rodriguez *et al.* (1993) described size selective predation pressure by brook trout (*Salvelinus fontinalis*) which reduced the abundance of *Holopedium* of >1.2 mm body length by 76 – 81 %. Similarly, removal of Arctic charr (*Salvelinus alpinus*) from Lake Takvatn in north Norway resulted in an increase in density and biomass of *Holopedium* (Dahlhansen, 1995). The distinct paucity of potential prey in the pelagic zone in Loch Ness induces the planktivorous fish - Arctic charr and to a lesser extent three-spine sticklebacks (*Gasterosteus aculeatus*) and brown trout to be trophically opportunistic. One might therefore hypothesise that a relatively large and immobile prey 'package' of *Holopedium* should be actively selected, compared to the more abundant but smaller and agile copepod species. Thackeray *et al.* (2000) quantified the degree of feeding selectivity exhibited by brown trout in Loch Ness using a selectivity index (Ivlev, 1961). Despite *Holopedium* occurring in comparable numbers to *Bythotrephes* in the water column, the results of gut content analyses showed negative selection, or avoidance of *Holopedium* by brown trout, whilst *Bythotrephes* was actively selected. Arctic charr from Loch Ness exhibited a similar trait (Martin & Shine, 1993) and comparable results were observed in studies on similar fish species in oligotrophic lakes in Canada and Scandinavia (Coulas *et al.*, 1998; Dervo *et al.*, 1991; Hegge *et al.*, 1993). The lack of evidence for ingested *Holopedium* appearing in the gut may be a function of the fragility of the organism. *Daphnia* species and the copepods have robust carapace structures which are readily identifiable in gut content analysis, whilst *Bythotrephes* has a long caudal spine that proves a most recalcitrant indicator of abundance. The protective mantle replaces the need for a robust carapace structure in *Holopedium* and the body may thus succumb to the mechanical pressures of ingestion. Since four independent observers were unable to find significant traces of *Holopedium* in the gut contents of three planktivore species from Loch Ness, it is unlikely that the disparity is due to observer error. Unless the zooplankters have only just reached the gut, observers may be unable to accurately assess the contribution of *Holopedium* to the diet. Alternatively, the mucopolysaccharide mantle may increase the likelihood of fish regurgitating recently ingested prey

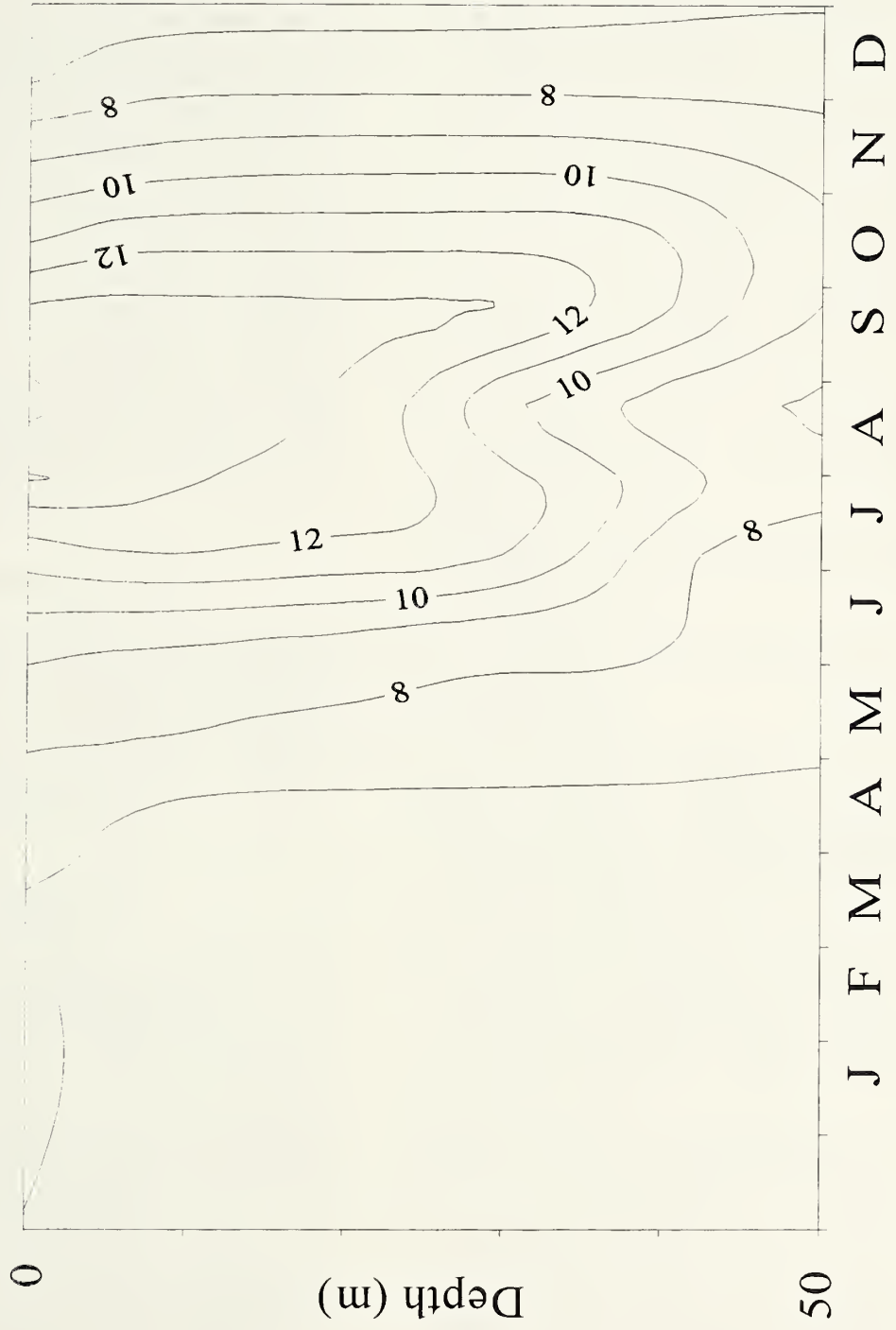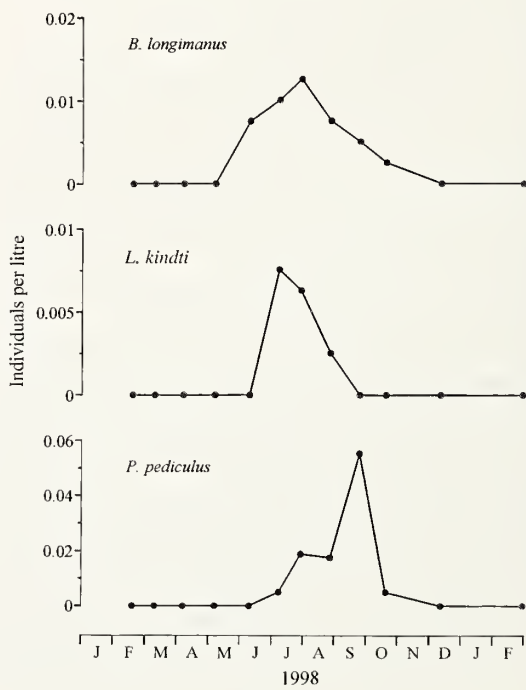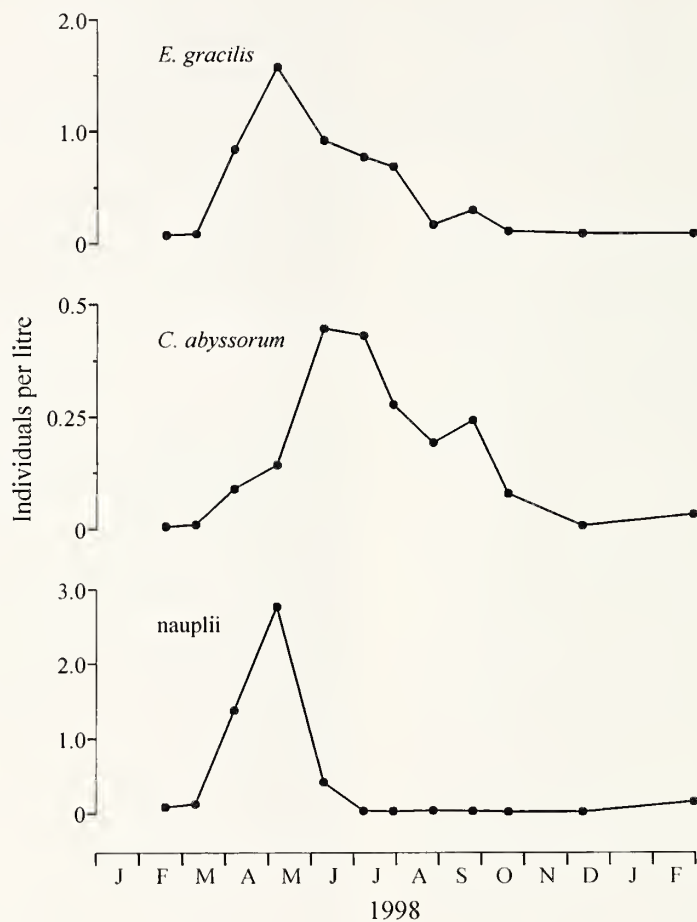Figure 1. Isothermal plot of the top 50 metres of the Loch Ness water column during 1998.

Figure 2. Seasonal abundance (zooplankton per litre) of (a) copepods - top middle , (b) grazing cladocerans - lower left, and (c) predatory cladocerans from the top 30 metres of the Loch Ness water column during 1998 - lower right.

under the stress of capture of the fish although this is purely speculative.

Stable isotope analysis (SIA) is proving a powerful tool to ecologists investigating trophic relationships as it more accurately assesses the long term assimilated diet of an organism. The technique relies on tracing ratios of naturally occurring isotopes (usually carbon and nitrogen 'signatures') from one organism to another because the transfer between each trophic level is predictable (Hobson, 1999). However, to effectively utilise the SIA technique, the source end-points must be robust and significantly distinct from each other. Since *Daphnia* and *Holopedium* have very similar modes of feeding and both are apparently grazing the late summer algal production, they both exhibit similar isotopic signatures (Grey *et al.*, 2000a). Therefore, from the seasonality of the plankton dynamics and from the isotopic evidence, it appears that *Holopedium* is an important consumer of autochthonous production in Loch Ness during the late summer. However, despite detailed gut content and stable isotope analyses, the contribution of *Holopedium* to the diet of planktivores and hence the importance of this zooplankter as a link to higher trophic levels in the Loch Ness food web remains something of a mystery.

ACKNOWLEDGEMENTS

REFERENCES

Campbell, C.E. (1991). Prey selectivities of threespine sticklebacks (*Gasterosteus-aculeatus*) and phantom midge larvae (*Chaoborus* Spp) in Newfoundland Lakes. *Freshwater Biology* **25**, 155-167.

Coulas, R.A., MacIsaac, H.J. & Dunlop, W. (1998). Selective predation on an introduced zooplankter (*Bythotrephes cederstroemi*) by lake herring (*Corregonus artedii*) in Harp Lake, Ontario. *Freshwater Biology* **40**, 343-355.

Cyr, H. (1998). Cladoceran- and copepod-dominated zooplankton communities graze at similar rates in low-productivity lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 414-422.

Cyr, H. and Curtis, J.M. (1999). Zooplankton community size structure and taxonomic composition affects size-selective grazing in natural communities. *Oecologia* **118**, 306-315.

Dahlhansen, G. (1995). Long term changes in crustacean zooplankton – the effects of a mass removal of arctic charr, *Salvelinus alpinus* (L.) from an oligotrophic lake. *Journal of Plankton Research* **17**, 1819-1833.

Dervo, B.K., Hegge, O., Hessen, D.O. & Skurdal, J. (1991). Diel food selection of pelagic Arctic charr, *Salvelinus alpinus* (L.) and brown trout, *Salmo trutta* (L.), in Lake Atnsjo, SE Norway. *Journal of Fish Biology* **38**, 199-209.

Eggers, D.M. (1977). The nature of prey selection by planktivorous fish. *Ecology* **58**, 46-59.

Fryer, G. (1991). *A natural history of the lakes, tarns and streams of the English Lake District.* The Freshwater Biological Association, Cumbria, UK.

Grey, J., Jones, R.I. & Sleep, D. (2000a). The importance of allochthonous carbon to the diet of zooplankton in Loch Ness revealed by stable isotope analysis: a seasonal overview. *Limnology & Oceanography* under review.

Grey, J., Thackeray, S.J., Jones, R.I. & Shine, A. (2000b). Ferox trout as 'Russian Dolls': trophic links at the top of the Loch Ness food web. *Oikos* under review.

Hegge, O., Hesthagen, T. & Skurdal, J. (1993). Vertical distribution and substrate preference of brown trout in the littoral zone. *Environmental Biology of Fishes* **36**, 17-24.

Hobson, K.A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* **120**, 314-326.

Ivlev, V.S. (1961). *Experimental ecology of the feeding of fishes.* Yale University Press.

Jones, R.I., Fulcher, A.S., Jayakody, J.K.U., Laybourn-Parry, J., Shine, A., Walton, M.C. & Young, J.M. (1995). The horizontal distribution of plankton in a deep oligotrophic lake – Loch Ness, Scotland. *Freshwater Biology* **33**, 161-170.

Jones, R.I., Grey, J., Sleep, D. & Quarmby, C. (1998). An assessment, using stable isotopes, of the importance of allochthonous organic carbon sources to the pelagic food web in Loch Ness. *Proceeding of the Royal Society London B* **265**, 105-111.

Jones, R.I., Laybourn-Parry, J., Walton, M.C. & Young, J.M. (1997). The forms and distribution of carbon in a deep, oligotrophic lake (Loch Ness, Scotland). *Verhandlungen der Internationale Vereinigung Für Theoretische und Angewandte Limnologie* **26**, 330-334.

Jones, R.I., Young, J.M., Hartley, A.M. & Bailey-Watts, A.E. (1996) Light limitation of phytoplankton development in an oligotrophic lake – Loch Ness, Scotland. *Freshwater Biology* **35**, 533-543.

Lampert, W. & Sommer, U. (1997). *Limnoecology: The Ecology of Lakes and Streams.* Oxford University Press.

Laybourn-Parry, J. & Walton, M. (1998). Seasonal heterotrophic flagellate and bacterial plankton dynamics in a large oligotrophic lake – Loch Ness, Scotland. *Freshwater Biology* **39**, 1-8.

Maitland, P.S., Smith, B.D. & Dennis, G.M. (1981) The crustacean zooplankton. Pp. 135-154 in Maitland, P.S. (editor) *The Ecology of Scotland's Largest Lochs, Monographiae Biologicae* **44**. Dr W. Junk Publishers, The Hague.

Martin, D.S. & Shine, A. (1993). The food and feeding relationships of pelagic fish in Loch Ness. *The Scottish Naturalist* **105**, 149-174.

O'Brien, W.J., Kettle, D. & Reissen, H. (1979). Helmets and invisible armor: structures reducing predation from tactile and visual planktivores. *Ecology*, **60**, 287-294.

Rodriguez, M.A., Magnan, P. & Lacasse, S. (1993). Fish species composition and lake abiotic variables in relation to the abundance and size strcuture of cladoceran zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 638-647.

Scourfield, D.J. & Harding, J.P. (1966). A key to the British species of freshwater Cladocera. *Freshwater Biological Association, Scientific Publication No.5.*

Tessier, A.J. (1983). Coherence and horizontal movements of patches of *Holopedium* gibberum (Cladocera). *Oecologia* **60**, 71-75.

Thackeray, S.J., Grey, J. & Jones, R.I. (2000). Feeding selectivity in brown trout (*Salmo trutta*) in Loch Ness, Scotland. *Freshwater Forum* **13**, 47-59.

The Scottish Naturalist (1993). Collected Papers on Loch Ness Research initiated by the Loch Ness and Morar Project. Volume **105** (1-3).

Wahlström, E. & Westman, E. (1999). Planktivory by the predacious cladoceran *Bythotrephes longimanus*: effects on zooplankton size structure and abundance. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1865-1872.

Young, J.M., Laybourn-Parry, J., Jones, R.I. & Walton, M. (1995). A stalkless sub-species of *Clathrulina elegans* Cienkowski (1867) from the plankton of Loch Ness, Scotland. *European Journal of Protistology* **31**, 54-57